

# 1 Plant Neighbourhood Diversity Effects on Leaf Traits: A Meta- 2 analysis

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## 7 **Data availability**

8 The data and code used in this meta-analysis is available on GitHub ([https://github.com/JuriFelix/leaf-  
9 trait-meta-analysis/](https://github.com/JuriFelix/leaf-trait-meta-analysis/)).

## 10 **Acknowledgements**

11 The authors would like to thank Raquel Benavides, Bastien Castagneyrol, Andréa Davrinche, Olga  
12 Ferlian, Estelle Forey, Melanie Gibbs, Hervé Jactel, Tobias Proß, Laura Williams and Fabienne Zeugin  
13 for contributing additional data and unpublished results to this meta-analysis. This work was  
14 supported by the Biotechnology and Biological Sciences Research Council (BBSRC) through grant  
15 BB/M011178/1.

## 16 **Author contributions**

17 JK and JAF designed this research; JAF extracted data from studies and conducted the analysis; JAF  
18 and JK wrote the manuscript with contributions from PCS.

## 19 **Conflicts of interest**

20 The authors have no conflict of interest.

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## 25 **Abstract**

- 26 1. Leaf traits often vary with plant neighbourhood composition, which in turn may mediate plant  
27 susceptibility to herbivory. However, it is unknown whether there are any common patterns  
28 of change in leaf trait expression in response to neighbourhood diversity, and whether these  
29 responses confer increased resistance or susceptibility to herbivores.
- 30 2. We used meta-analysis to combine data from 43 studies that examined the influence of  
31 neighbourhood diversity on eight physical and chemical leaf traits that could affect herbivory.  
32 All leaf traits apart from leaf thickness were highly plastic and exhibited significant differences  
33 between plant monocultures and species mixtures, but the direction of effect was variable.  
34 Leaf toughness was the only trait that displayed a significant decrease with plant diversity,  
35 whereas specific leaf area (SLA) and leaf nitrogen were both marginally increased in species  
36 mixtures.
- 37 3. The magnitude and direction of leaf trait responses to neighbourhood diversity were  
38 independent of plant density and phylogenetic diversity, but changes in SLA correlated  
39 positively with plant species richness. SLA was also significantly increased in experimental  
40 studies, but not in observational studies, while neighbourhoods containing nitrogen-fixers  
41 were associated with increased leaf nitrogen and reduced phenolics. When studies on the  
42 over-represented species *Betula pendula* were removed from the analysis, the effect of  
43 neighbourhood diversity on leaf toughness became non-significant, but phenolics were  
44 significantly reduced in diverse neighbourhoods composed of mature trees, and marginally  
45 reduced in species mixtures across all studies.
- 46 4. Increases in plant neighbourhood diversity are often associated with reductions of herbivory,  
47 although in some cases the reverse occurs, and plants growing in species mixtures are found  
48 to suffer greater herbivory than those in monocultures. This study offers a potential  
49 explanation for the latter phenomenon, as our results show that leaf trait expression is highly  
50 plastic in response to neighbourhood diversity, and in certain cases could lead to increased  
51 leaf quality, which in turn could promote greater rates of herbivory.

52 **Key words:** associational effects, BEF, defence, insect herbivore, leaf traits, meta-analysis  
53 neighbourhood diversity

## 54 **Introduction**

55 Plants growing in mixed-species neighbourhoods are often subject to lower rates of herbivory than  
56 those growing in monocultures (Jactel et al., 2021). The mechanisms frequently attributed to this  
57 phenomenon include reduced host plant apparency and increased regulation of herbivores by

58 predators and parasitoids (Barbosa et al., 2009; Guyot et al., 2016; Jactel et al., 2021; Letourneau et  
59 al., 2011; Root, 1973; Stemmelen et al., 2022). However, these mechanisms are unable to account for  
60 the results of numerous studies that have documented increased rather than decreased herbivory in  
61 diverse neighbourhoods, which suggests that additional factors are involved in determining the  
62 strength and direction of plant neighbourhood effects on herbivores (Barbosa et al., 2009; Berthelot  
63 et al., 2021; Jactel et al., 2021; White & Whitham, 2000). One such factor that has been increasingly  
64 explored is the intraspecific variation in physical and chemical leaf traits of the focal plant in different  
65 neighbourhoods, that can in turn influence leaf quality and rates of herbivory (Mraja et al., 2011;  
66 Poeydebat et al., 2020; Rosado-Sánchez et al., 2018a). Understanding the patterns of leaf trait  
67 variation in heterospecific vs conspecific neighbourhoods may offer additional insights into the  
68 variability of neighbourhood diversity effects on herbivores, as well as other processes that are  
69 mediated by neighbourhood diversity (Cardinale et al., 2007; Hong et al., 2021).

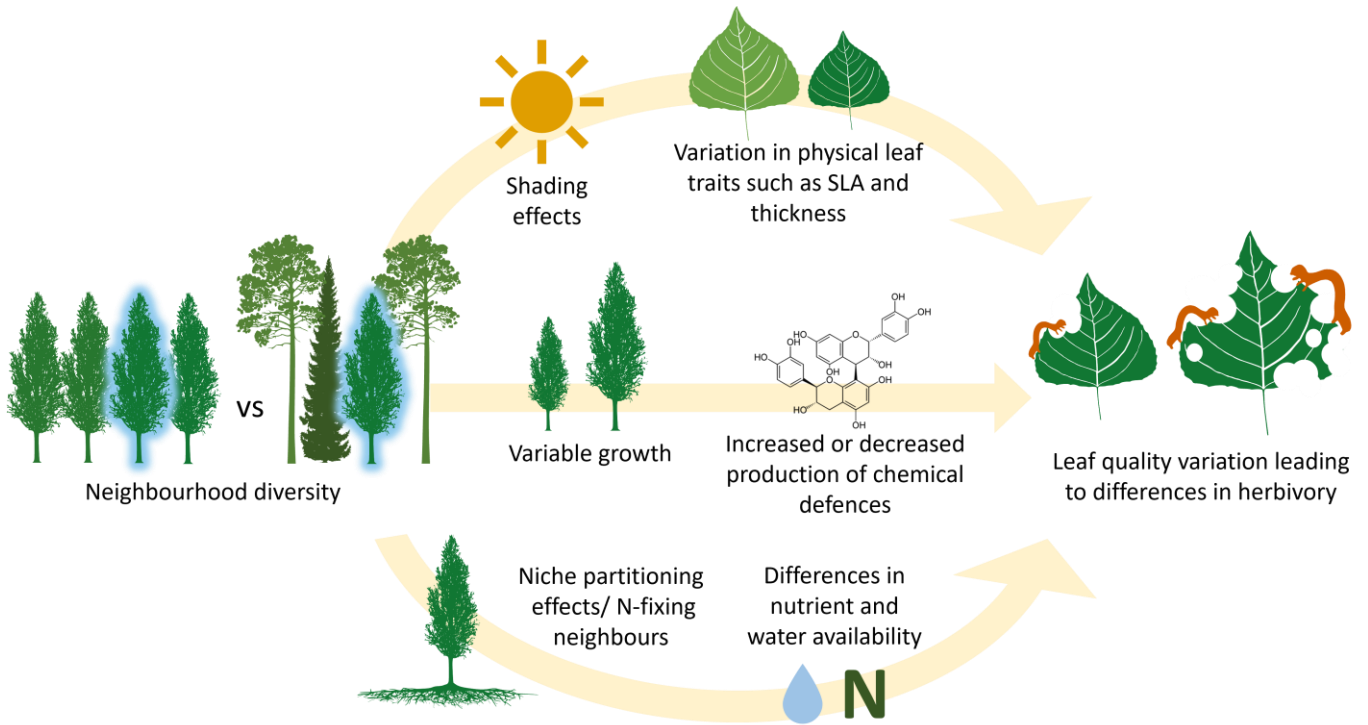
70 Leaf traits are highly plastic to the variation in biotic and abiotic conditions in different plant  
71 neighbourhoods due to the distinct morphologies, canopy structures, and resource requirements of  
72 different species (Callaway et al., 2003; Pretzsch, 2014; Rozendaal et al., 2006). Changes in leaf traits  
73 can affect leaf quality to herbivores, and hence increase or decrease the amount of herbivore damage  
74 received (Figure 1) (Awmack & Leather, 2002; Carmona et al., 2011; Castagneyrol et al., 2018; Moreira  
75 et al., 2016; Rosado-Sánchez et al., 2018b). For example, fast-growing neighbours in species mixtures  
76 can increase canopy stratification and the amount of shading experienced by a focal plant, which  
77 might result in a higher specific leaf area (SLA) and lower leaf thickness as an adaptation to maximise  
78 photosynthesis in a light limited environment (Reich et al., 1997; Roberts & Paul, 2006; Williams et al.,  
79 2020). This in turn may increase the palatability of leaves to herbivores, as leaves with higher SLA are  
80 more tender and easier to digest (Muiruri et al., 2019). Likewise, the nutritional value of leaves may  
81 vary with the availability of nitrogen in the soil, that can be boosted through the presence of  
82 neighbouring nitrogen-fixing plants (N-fixers) in species mixtures (Richards et al., 2010).

83 Diverse neighbourhoods may also increase resource-use complementarity, leading to niche-  
84 partitioning effects, that can reduce competition for space and nutrients. If these mechanisms result  
85 in increased resource uptake in species mixtures as compared to monocultures, plants in species  
86 mixtures might experience more vigorous growth and increase their investment into chemical and  
87 physical defences (Cardinale et al., 2007; Isbell et al., 2017; Loreau & Hector, 2001; Potvin & Gotelli,  
88 2008). Alternatively, growth-defence trade-offs could lead to lower levels of defences in plants with

89 increased vigour (Herms & Mattson, 1992), however, evidence for such trade-offs in diverse  
90 neighbourhoods has been limited (Abdala-Roberts et al., 2014; Moreira et al., 2014).

91

92 **Figure 1:** Conceptual diagram showing the ways that neighbourhood diversity can influence leaf



93 quality. Light intensity, nutrient and water availability, and individual tree growth may all vary with  
94 neighbourhood diversity, which can cause variation in leaf traits and lead to increased or decreased  
95 leaf quality. Differences in leaf quality can in turn lead to variation in herbivory.

96 Leaf trait variation in response to neighbourhood diversity has increasingly been investigated in  
97 grassland and forest diversity experiments, but results have been highly variable, with leaf traits  
98 including SLA, phenolic compounds and foliar nitrogen increasing, decreasing, or not changing  
99 significantly between focal plants growing in monocultures and species mixtures (Castagneyrol et al.,  
100 2019; Kostenko et al., 2017; Poeydebat et al., 2020; Wäschke et al., 2015; Williams et al., 2020).  
101 Furthermore, plant ontogeny, planting density and the presence of specific neighbour plants such as  
102 N-fixers can also influence leaf traits, and may obscure overall neighbourhood diversity effects (Barton  
103 & Koricheva, 2010; Benavides et al., 2019; Guyot et al., 2016; Moreira et al., 2017; Richards et al.,  
104 2010; Tobner et al., 2014).

105 Neighbourhood effects may also depend on the species richness and the phylogenetic diversity of the  
106 plant mixture. As species richness increases, so does the number of unique plant-plant interactions

107 and of biotic and abiotic environments experienced by a focal plant. The phylogenetic diversity of a  
108 neighbourhood can have similar influences, where more phylogenetically diverse species mixtures  
109 (e.g. pine-oak mixture, as opposed to a mixture of two oak species) are predicted to harbour more  
110 heterogenous biotic and abiotic environments due to the greater diversity of plant niches and growth  
111 patterns (Jactel et al., 2021; Williams et al., 2020).

112 To identify general patterns of trait responses to neighbourhood diversity we conducted a meta-  
113 analysis of studies that compared leaf traits in monocultures and species mixtures. We assessed the  
114 responses of leaf thickness, toughness, leaf dry matter content (LDMC), terpenoids, phenolics, carbon  
115 (C), specific leaf area (SLA), and nitrogen (N). We chose to focus on traits that have been shown to  
116 influence chewing insects as they have received the most attention in neighbourhood diversity studies  
117 (Jactel et al., 2021). We expect that increases of SLA and N would increase leaf quality for chewers,  
118 whereas increases of the other six traits assessed would decrease leaf quality (Farmer, 2014; Gardarin  
119 et al., 2014; Schädler et al., 2003).

120 Sources of variation in leaf trait responses were elucidated by assessing the influences of plant species  
121 richness, phylogenetic diversity, presence of nitrogen-fixers, planting density, ontogeny, and  
122 experimental design in meta-regression models. Our analysis aimed to answer the following  
123 questions:

- 124 • Does leaf trait expression differ for plants growing in species mixtures compared to those  
125 growing in monocultures?
- 126 • Does the direction and/or magnitude of response to neighbourhood diversity differ between  
127 individual leaf traits?
- 128 • Do leaf trait responses to neighbourhood diversity depend on plant density, species richness,  
129 phylogenetic diversity, presence of nitrogen-fixing neighbours, ontogeny, and experimental  
130 design?

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## 136 **Materials and methods**

### 137 **Literature search and screening**

138 SCOPUS and the Web of Science Core Collection were searched for relevant publications in January  
139 2021 using the following search string:

140 (“plant” OR “tree” OR “crop”) AND (“divers\*” OR “intercrop\*” OR “species rich\*” OR “monoculture”  
141 OR “polyculture” OR “cultivar mixture\*” OR “neighbo?r\*”) AND (“VOC” OR “defen?e” OR “trichome”  
142 OR “secondary metabolite\*” OR “leaf chemi\*” OR “plant quality\*” OR “phytochem\*” OR “volatile\*”  
143 OR “resistance” OR “leaf trait” OR “plant trait”) AND “herbivor\*”.

144 Articles published in English were retained, yielding 2381 and 2064 results from the two databases,  
145 respectively. A further 24 papers were identified through checking the reference lists of papers  
146 identified through the database search, as well as from relevant review papers. Moreover, the list of  
147 publications on the TreeDivNet website (<https://treedivnet.ugent.be/index.html>) was checked, and  
148 members of the network were sent requests for unpublished data. This yielded 18 additional papers  
149 and datasets. Finally, several studies included in a previous meta-analysis by Richards et al. (2010) that  
150 had investigated foliar nitrogen levels of trees in monocultures and species mixtures were integrated  
151 into this meta-analysis.

152 All article titles and abstracts were screened, and irrelevant studies where leaf traits were not  
153 measured were excluded. The full text of the remaining articles was then examined, and studies that  
154 fitted the following inclusion criteria were retained to be used in the meta-analysis (see Figure S1 in  
155 Supporting Information)

156 a) Plant traits that could influence herbivory were measured on undamaged leaves for a focal plant  
157 species growing within monocultures and species mixtures, with other factors such as plant ontogeny,  
158 time of year, and stand density remaining constant between different plots. Only studies on  
159 constitutive leaf traits were considered.

160 b) Mean values of trait measurements, standard errors or standard deviations, and sample sizes were  
161 reported in the paper or in the supplementary information or were available upon request from the  
162 authors.

163 c) Data was gathered from a minimum of two replicate plots for monocultures and each species  
164 mixture.

165 While the original literature search extended to all plant traits, the majority of relevant papers  
166 provided data on leaf traits and hence the subsequent analysis was restricted to plant diversity effects

167 on eight leaf traits: specific leaf area (SLA), leaf dry matter content (LDMC), thickness, toughness, total  
168 nitrogen (N), total carbon (C), phenolic compounds, and terpenoid compounds. The canopy layer from  
169 which leaves were sampled differed between studies (e.g. lower branches, sun leaves or a mixture of  
170 different positions) but was consistent between monoculture and species mixture sampling within  
171 each study. Phenolics and terpenoids represent large classes of plant secondary compounds that share  
172 a common biosynthetic pathway; in our analysis terpenoids include data on monoterpenes,  
173 sesquiterpenes, diterpenes and iridoid glycosides, whereas phenolics include flavonoids, lignins,  
174 condensed tannins, hydrolysable tannins and measurements of total phenolics. Due to insufficient  
175 data, responses of individual compounds could not be considered, however there were sufficient  
176 effect sizes to examine the effects of neighbourhood diversity on the four subgroups of phenolic  
177 compounds mentioned above as well as 'total phenolics'.

178 To investigate sources of variation among effect sizes, data for the following moderators was also  
179 extracted from each publication: plant species richness for each species mixture; planting density (only  
180 for woody plants); study design (experimental vs observational); plant ontogenetic stage (only for  
181 woody plants); and presence of nitrogen-fixing species in a mixture. Additionally, the identity of all  
182 focal and neighbouring species within each study was used to calculate average phylogenetic diversity  
183 values for each plot (see Methods S1 for details).

#### 184 **Effect size calculations**

185 All statistical analyses were conducted in R version 4.04 (R Core Team, 2021) using the package  
186 *metafor* version 3.4 (Viechtbauer, 2010). Effect sizes were calculated as a standardised mean  
187 difference (SMD, Hedges' *g*) (Gurevitch & Hedges, 1993) between the mean value of a leaf trait of a  
188 focal species in a species mixture and that in a monoculture. Positive SMD values indicated that the  
189 leaf trait value was higher for focal plants growing in species mixtures compared to monocultures. As  
190 we expected the direction of the effect to be highly context-dependent (i.e. different neighbours may  
191 cause either an increase or a decrease in the same leaf trait), we also calculated absolute value effect  
192 sizes (hereafter referred to as absolute effect sizes) by removing the sign from all SMD values. This  
193 allowed us to compare the magnitude of the effect of neighbourhood diversity on different plant  
194 traits.

195 If traits were measured for a focal plant species in several different mixture types (e.g. monoculture,  
196 2, 4 and 8-species mixtures) then the same monoculture values would be used as a control for each  
197 of the mixture types. When data were presented on a graph, mean values and SD/SE were extracted  
198 using the software WebPlotDigitizer (<https://automeris.io/WebPlotDigitizer/>). When only standard

199 errors were reported, they were transformed to standard deviations by multiplying them by the  
200 square root of the sample size.

201 If studies reported correlations between leaf trait values and plant species richness instead of mean  
202 values for monocultures and species mixtures, SMD ( $d$ ) and variance ( $V_d$ ) values were approximated  
203 using the following formulae derived from Borenstein, (2009) (Methods S1). A total of 1007 effect  
204 sizes from 43 studies were included in the final meta-analysis. Distribution of directional and absolute  
205 effect sizes for each trait was visualized using orchard plots (Nakagawa et al., 2021).

## 206 **Meta-analysis**

207 Multi-level model analysis was performed using the 'rma.mv' function in *metafor*. Study ID,  
208 experimental site, individual effect ID, and plant species were included as random factors to control  
209 for non-independence among effect sizes (Table S11) (Nakagawa et al., 2017; Noble et al., 2017). To  
210 account for phylogenetic non-independence arising from relatedness among focal species, the R  
211 package *rotf* (Michonneau et al., 2016) was used to create a phylogenetic correlation matrix of all focal  
212 species in the meta-analysis that was then linked to an additional phylogeny random factor (Cinar et  
213 al., 2022; Nakagawa & Santos, 2012).

214 The overall effect of neighbourhood diversity on each leaf trait of a focal plant species was assessed  
215 by calculating the grand mean effect sizes of the SMD. An effect was considered significant if the 95%  
216 confidence intervals did not overlap with zero (Koricheva et al., 2013). To explore sources of  
217 heterogeneity, moderators were incorporated into analysis models for traits with sufficient numbers  
218 of effect sizes (Nakagawa et al., 2017), which in this study included C, N, SLA, LDMC, and phenolics.  
219 Moderator interactions were not included due to insufficient sample sizes.

220 Absolute effects of neighbourhood diversity on leaf traits were calculated by repeating the meta-  
221 analysis and meta-regression models with the sign removed from all effect sizes. This technique has  
222 been utilised in previous meta-analyses to compare the magnitudes of effects where the direction of  
223 effects was variable (e.g. Bailey et al., 2009; Champagne et al., 2016; Clements et al., 2022), and was  
224 used here to assess the degree of plasticity of different leaf traits in response to neighbourhood  
225 diversity, regardless of the direction of response.

226 Publication bias for each trait type was assessed by constructing funnel plots and inspecting them for  
227 asymmetry. In addition, we ran meta-regression models with sampling error or publication year as  
228 moderators to test for small study biases and decline effects, respectively (Nakagawa et al., 2022).  
229 Potential biases due to over-represented plant species were investigated by calculating the proportion  
230 of effect sizes derived from each plant species; those that contributed > 10% of effect sizes for a



231 specific trait were considered to be over-represented. Sensitivity analyses were then run to test the  
232 impact of these species by testing whether the results changed when these species are excluded from  
233 analysis.

## 234 **Results**

### 235 **Description of the dataset**

236 Phenolics, N, C, LDMC and SLA were the leaf traits most reported in studies looking at the effects of  
237 plant species richness (Table 1). Neighbourhood diversity was experimentally manipulated in most  
238 studies (85% of the data) and the majority of data (90% of effect sizes from 32 studies) came from  
239 studies on trees, with only 10% of effect sizes from 11 studies reporting effects of neighbourhood  
240 diversity on leaf traits in herbaceous plants. 125 focal plant species were represented in the dataset,  
241 but silver birch (*Betula pendula*) was highly over-represented and contributed 26% of all effect sizes.  
242 Studies exploring effects of plant diversity on leaf traits had an uneven global distribution, with 57%  
243 of effect sizes coming from temperate biomes, 16% from boreal biomes, and 27% from tropical and  
244 subtropical biomes (mainly from the subtropical BEF-China experiment, see Figure S2 for details).

### 245 **Mean directional and absolute effects of neighbourhood diversity on plant traits**

246 Leaf toughness was the only leaf trait that displayed a significant directional change with plant  
247 diversity; focal plant leaves were on average tougher in monocultures than in species mixtures,  
248 whereas SLA and leaf nitrogen both showed a marginally significant positive response to  
249 neighbourhood diversity (Table 1, Figure 1a). The 95% prediction intervals for most traits were broad,  
250 showing a high level of heterogeneity. When phenolics were analysed separately by class, none of the  
251 phenolic classes showed significant directional responses to neighbourhood diversity, although total  
252 phenolics exhibited a marginally significant reduction (Figure. 2).

253 Analysis of absolute effect sizes showed that all leaf traits apart from leaf thickness exhibited  
254 significant differences between monocultures and mixtures (Table 1, Figure 1b). The largest absolute  
255 effects were seen for SLA followed by N, whereas leaf toughness and phenolics showed the smallest  
256 absolute changes (Table 1).

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261 **Table 1:** Mean directional and absolute effect sizes showing standardised mean differences in leaf  
 262 traits between diverse neighbourhoods and monocultures. Effects were considered significant if 95%  
 263 confidence intervals (95 % CI) did not overlap with zero. 95 % PI = prediction interval that estimates  
 264 the range in which effect sizes of 95 % of future studies would be expected to fall, N = number of  
 265 studies from which data was extracted for each trait data, *k* = number of individual effect sizes for  
 266 each trait. Significant effects are shown in bold, marginally significant effects in italics.

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Trait	<i>k</i> (N)	Effect, 95% CI	95% PI	Absolute effect, 95 % CI	Absolute 95% PI
Thickness	20 (3)	-0.05 [-1.69; 1.60]	[-2.85; 2.76]	0.72 [-0.24; 1.68]	[-0.87; 2.31]
Toughness	20 (3)	<b>-0.40 [-0.72; -0.08] *</b>	[-0.72; -0.08]	<b>0.44 [ 0.12; 0.75] **</b>	[0.12; 0.75]
LDMC	119 (9)	-0.10 [-0.70; 0.51]	[-1.94; 1.74]	<b>0.66 [ 0.35; 0.98] ***</b>	[0.12; 1.21]
SLA	251 (17)	<b>0.46 [-0.03; 0.95]</b>	[-1.53; 2.45]	<b>1.04 [ 0.72; 1.35] ***</b>	[0.16; 1.91]
Terpenoids	24 (6)	-0.12 [-1.06; 0.82]	[-2.01; 1.77]	<b>0.70 [ 0.15; 1.26] *</b>	[-0.28; 1.68]
Phenolics	228 (13)	-0.07 [-0.27; 0.13]	[-0.72; 0.58]	<b>0.51 [ 0.36; 0.65] ***</b>	[0.20; 0.81]
Nitrogen	206 (27)	<b>0.23 [-0.03; 0.49]</b>	[-1.04; 1.50]	<b>0.83 [ 0.53; 1.13] ***</b>	[0.10; 1.57]
Carbon	139 (11)	-0.08 [-0.34; 0.18]	[-1.07; 0.92]	<b>0.68 [ 0.53; 0.83] ***</b>	[0.53; 0.83]

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280 **Meta-regressions for directional effects**

281 The only continuous variable that had a significant effect was species richness, where the positive  
282 effects of neighbourhood diversity on SLA were significantly stronger in mixtures with higher species  
283 richness (Table S2, Figure 4). SLA also showed significantly different responses depending on study  
284 type and tree age and was increased in diverse neighbourhoods in both experimental studies (Table  
285 S5) and studies of juvenile trees (Table S4). Nitrogen was likewise increased in mixtures of juvenile  
286 trees but, contrary to SLA, was significantly higher in mixed stands only in observational studies –  
287 although this is likely a statistical artifact due to low sample sizes. Focal trees in neighbourhoods  
288 containing N-fixers had decreased levels of phenolics and increased N levels as compared to  
289 monocultures (Table S3, Figure 4).

290 **Meta-regressions for absolute effects**

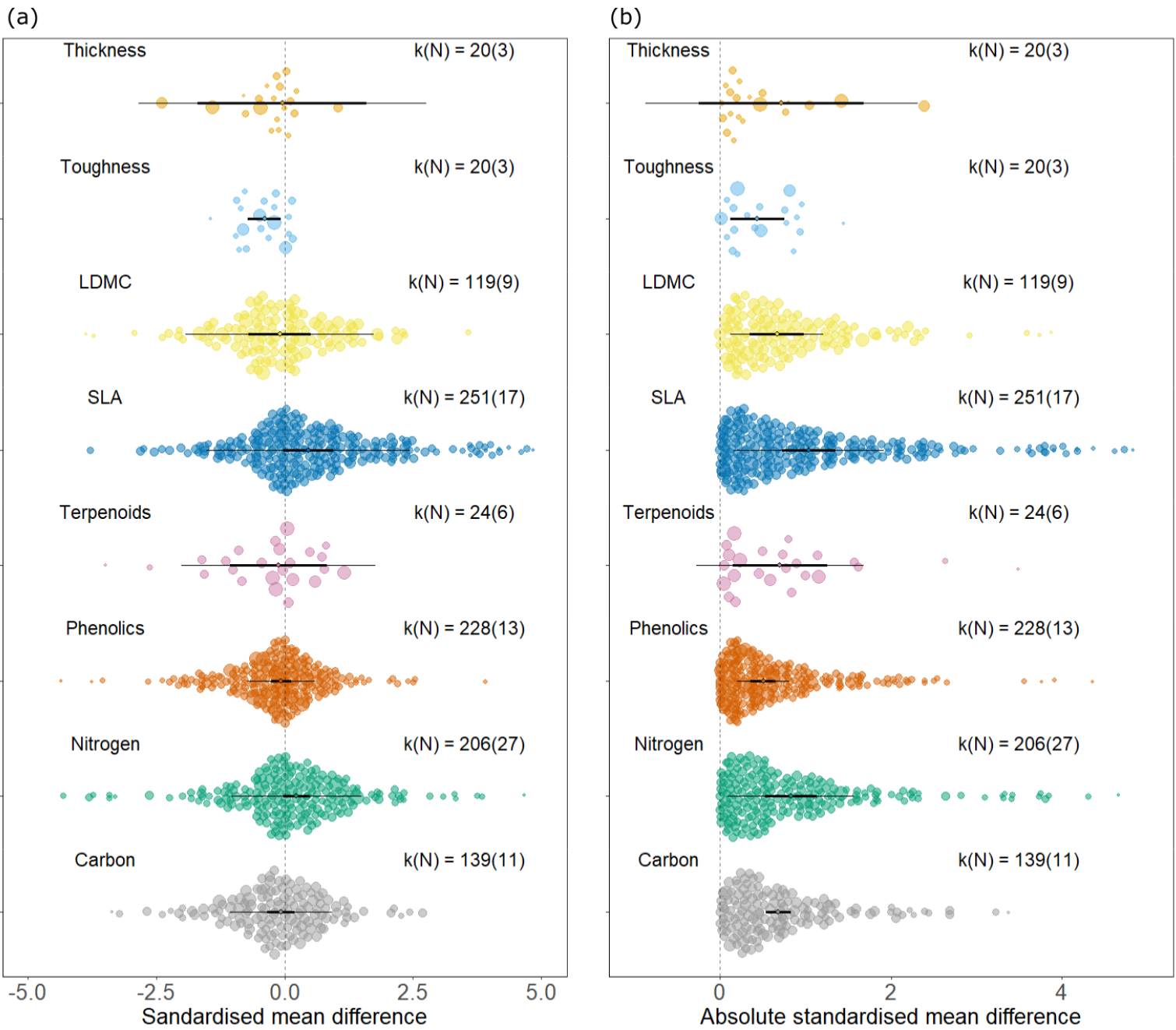
291 Absolute effect sizes for SLA and phenolics were significantly larger in experimental studies than in  
292 observational studies (Table S10), and effects on SLA exhibited marginally significant positive  
293 relationship with phylogenetic diversity (Table S7). Plant density, species richness, ontogenetic stage  
294 and the presence of N-fixing species had no significant effects on absolute magnitudes of leaf trait  
295 responses to neighbourhood diversity (Tables S7-S10).

296 **Sensitivity analysis and publication bias**

297 Due to the uneven distribution of moderators across studies, several of the categorical moderators  
298 were confounded. For instance, most studies that included N-fixing neighbours were experimental,  
299 and very few were observational. To account for this, meta-regressions were repeated with subgroups  
300 of effect sizes that were limited to one set of categorical moderators at a time (e.g. by comparing leaf  
301 trait responses to neighbourhood diversity in mature and juvenile trees only in experimental forests  
302 without N-fixing neighbours). There were no significant differences between these subsets and the  
303 meta-regressions that used the full dataset (results not shown), suggesting that confounded  
304 moderators did not lead to any erroneous conclusions.

305 Studies on silver birch (*Betula pendula*) were over-represented in this meta-analysis and contributed  
306 > 10 % of effect sizes for LDMC, C, N, phenolics, toughness, and thickness. When *B. pendula* was  
307 excluded, the reduction of leaf toughness in species mixtures was no longer significant, but the  
308 decrease in phenolics became marginally significant. The mean absolute effect for leaf toughness was  
309 also no longer significant when *B. pendula* effect sizes were excluded from analyses, while the mean  
310 absolute effect for leaf thickness became significant (see Table S10).

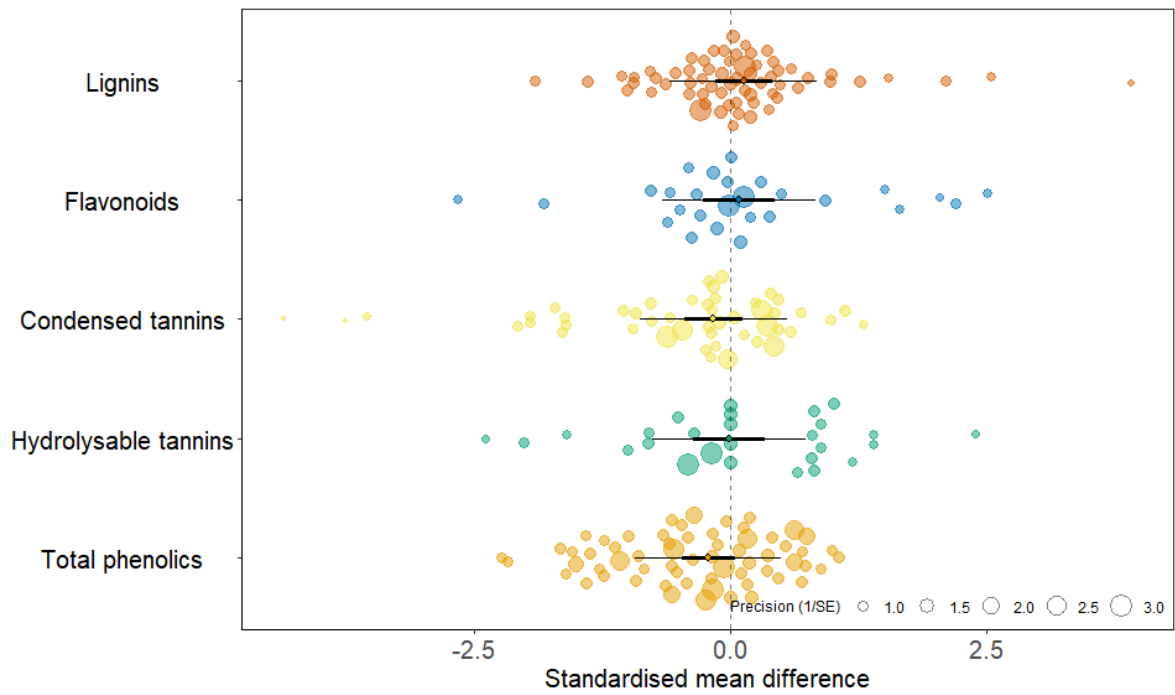
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314 **Figure 2:** Orchard plots of the directional (a) and absolute (b) effects of neighbourhood diversity on 8  
 315 leaf traits. N = number of studies from which data was extracted for each trait, k = number of individual  
 316 effect sizes for each trait, thick bars = 95 % confidence intervals (95 % CI), thin bars = 95 % prediction  
 317 intervals. Effects are considered significant if the 95 % CI does not overlap with zero.

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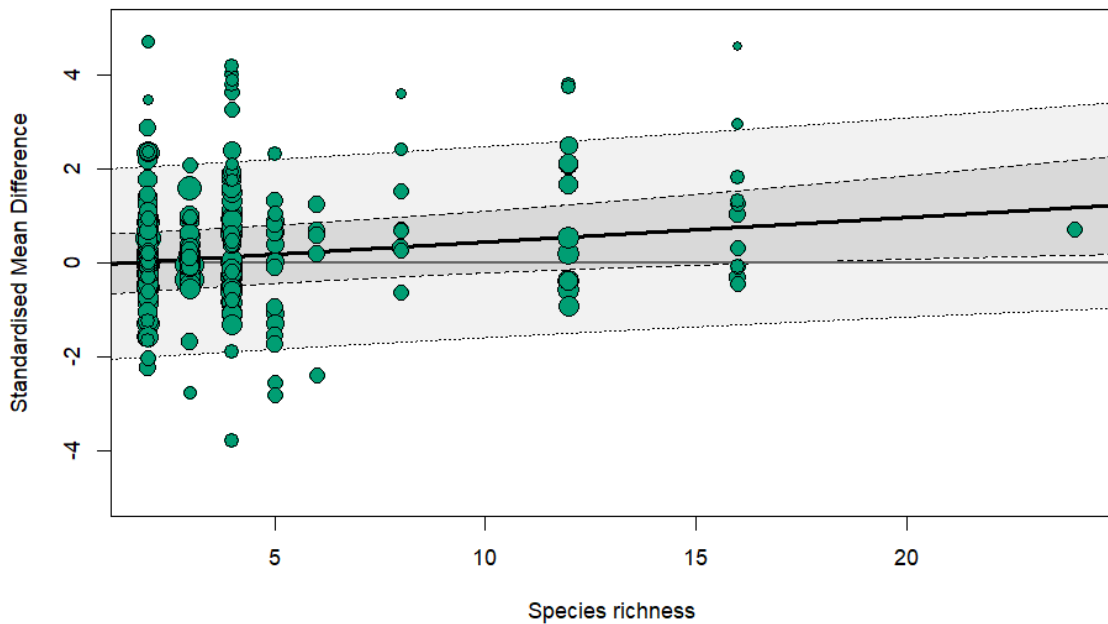


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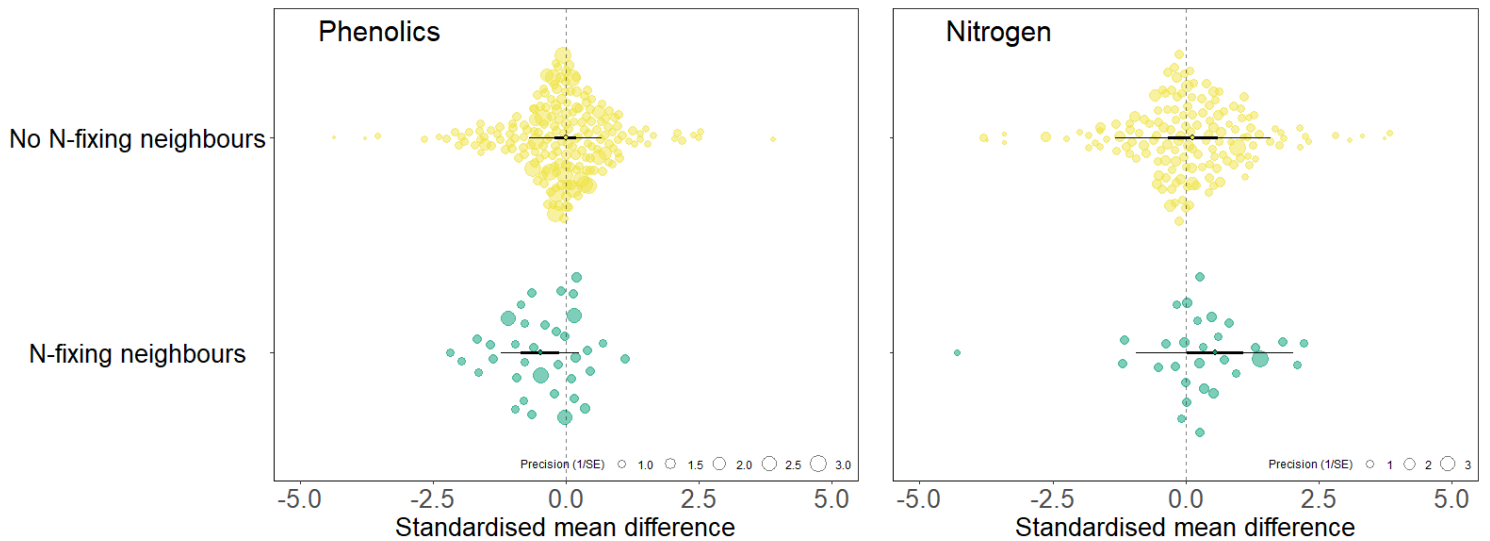
320 **Figure 3:** Orchard plots of the directional effects of neighbourhood diversity on 5 classes of phenolic  
 321 compounds. Thick bars = 95 % confidence intervals (95 % CI), thin bars = 95 % prediction intervals.

322 Effects are considered significant if the 95 % CI does not overlap with zero.

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324 **Figure 4:** Effect of the species richness of a mixture on the standardised mean difference value for  
 325 SLA. Black line = slope of the effect, dark grey area = 95 % confidence interval, light grey area = 95 %  
 326 prediction interval.



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328 **Figure 5:** Orchard plots of the effects of neighbourhood diversity on phenolics and leaf nitrogen in the  
 329 presence and absence of N-fixing neighbours. Thick bar = 95 % confidence interval (95 % CI), thin bar  
 330 = 95 % prediction interval. Effects are considered significant if the 95 % CI does not overlap with zero.

331 The removal of *B. pendula* effect sizes from meta-regressions on phenolics changed the outcome of  
 332 several models; phenolics in mature trees were significantly reduced in species mixtures (Juvenile = -  
 333 0.04 [-0.23; 0.16]  $k = 34$ , Mature = -0.23 [-0.44; -0.02],  $k = 33$ ,  $Q_m = 1.812$ ,  $p = 0.178$ ), while increasing  
 334 species richness had a marginal negative effect (intercept = -0.13 [-0.27; 0.01],  $k = 75$ ). Phenolics  
 335 remained significantly reduced in the presence of N-fixing species when *B. pendula* effect sizes were  
 336 excluded (N-fixing = -0.38 [-0.70; -0.06]  $k = 12$ , no N-fixing = -0.08 [-0.22; 0.06]  $k = 63$ ,  $Q_m = 2.818$ ,  $p$   
 337 = 0.093). Moreover, the difference in response of absolute effects for phenolics to neighbourhood  
 338 diversity in observational and experimental studies was no longer significant when *B. pendula* effect  
 339 sizes were removed ( $Q_m = 2.677$ ,  $p = 0.102$ ). Meta-regression results for LDMC, C and N were not  
 340 affected by the removal *B. pendula* effect sizes.

341 Visual inspection of funnel plots revealed no major asymmetries (Figure S3), however, the relationship  
 342 between effect sizes and sampling error was significantly negative for phenolics and significantly  
 343 positive for N and SLA (Figure S4a). No significant changes in effect sizes with publication year were  
 344 detected for any trait (Figure S4b).

## 345 Discussion

346 All but one of the examined leaf traits showed significant absolute differences between monocultures  
 347 and species mixtures, indicating high phenotypic plasticities of both physical and chemical leaf traits

348 in response to neighbourhood diversity. However, the only trait which displayed a significant mean  
349 directional response to neighbourhood diversity was leaf toughness. Taken together, these results  
350 suggest that the magnitude and direction of leaf trait responses to plant diversity are highly context-  
351 dependent and may contribute to either increased or decreased leaf quality for herbivores depending  
352 on the identity of the focal and neighbouring species.

### 353 **Individual leaf trait responses to neighbourhood diversity**

354 The largest absolute effects were observed for SLA and N, followed by C and LDMC, whereas smaller  
355 changes occurring for leaf toughness, phenolics and terpenoids. The high plasticity of SLA to  
356 neighbourhood diversity may reflect responses to light variation, where decreased light availability  
357 typically leads to greater SLA and thus greater light capture per unit mass, and the reverse occurs in  
358 high light conditions (Chapin et al., 2011; Reich et al., 1997; Williams et al., 2020). Increased canopy  
359 stratification and shading in species mixtures could increase SLA in shorter plants, while fast growing  
360 species such as *Betula* spp. may conversely experience higher SLA in monocultures where they are  
361 self-shaded by conspecifics (Poeydebat et al., 2020). LDMC, toughness and thickness are also known  
362 to vary with light levels (Valladares & Niinemets, 2008), albeit to a lesser extent than SLA (Rozendaal  
363 et al., 2006), which may explain their lower absolute mean effect sizes. Furthermore, different light  
364 conditions can also mediate variation in carbon-based chemical defences including phenolics and  
365 terpenoids, as well as total carbon, as a function of photosynthesis rates (Koricheva et al., 1998;  
366 Roberts & Paul, 2006).

367 While we found no significant differences between the neighbourhood diversity effects on different  
368 classes of phenolic compounds, significant variation in direction of response was observed in each  
369 group. To further explore this variation, future studies would benefit from including more detailed  
370 analysis of secondary metabolites, ideally making use of techniques that can identify specific  
371 compounds as has been done by chemical ecologists working in related fields (e.g. metabolomic-type  
372 approaches used by Sedio et al., 2017; Walker et al., 2022).

### 373 **Predictors of the leaf trait shifts**

374 Both shading and niche partitioning effects have been found to intensify at higher species richness  
375 levels (Davrinche & Haider, 2021; Pretzsch, 2014), which might offer an explanation for the increased  
376 response of SLA with species richness. While lower relative plasticities could explain the lack of  
377 response from other traits to species richness, effect sizes from plant neighbourhoods with high  
378 species richness (> 6) were derived from only four studies, thereby limiting the extent to which species  
379 richness effects could be examined.

380 Neighbourhood diversity effects in observational studies were expected to be weaker than in  
381 experimental studies due to reduced control of confounding environmental variables and the  
382 imperfect composition of monoculture plots (monocultures in observational studies are often defined  
383 as stands containing > 80-90 % of a given species). This was the case for SLA and phenolics, which  
384 showed significantly stronger absolute responses to neighbourhood diversity in experimental studies  
385 than they did in observational studies. Moreover, the directional shift in SLA was significantly higher  
386 in experimental studies than it was in observational studies.

387 Plant ontogenetic stage influences the expression of leaf traits and defences in plants (Barton &  
388 Koricheva, 2010) and may have an interactive effect with neighbourhood diversity (Moreira et al.,  
389 2017). The observed decrease in leaf phenolics in species mixtures of mature but not juvenile trees  
390 when over-represented *B. pendula* effect sizes were excluded suggests that phenolic compounds in  
391 mature trees are more responsive to neighbourhood effects. Alternatively, decreased phenolics in  
392 mature mixed stands of trees could result from stronger shading and complementarity effects relative  
393 to those in juvenile stands (Jucker et al., 2020; Lohbeck et al., 2013), however this isn't supported by  
394 the responses of both SLA and N, both of which were significantly increased in species mixtures  
395 composed of juvenile trees but not mature trees.

396 Leaf traits were predicted to be more responsive to neighbourhood diversity in stands of high density  
397 due to increased shading effects and tree-tree interactions (Pretzsch, 2014; Tobner et al., 2014).  
398 Although no overall effect of density was found in this analysis, much of the high-density data was  
399 taken from studies of juvenile trees that may not have grown large enough for canopy closure and  
400 notable niche-partitioning effects to occur.

401 Species mixtures with high phylogenetic diversity were also predicted to have a greater influence on  
402 leaf traits, as distantly related species are more likely to occupy different ecological niches, which  
403 could minimise competition and promote niche-partitioning effects. No significant effects of  
404 phylogenetic diversity on leaf trait responses to neighbourhood diversity were found in our analysis,  
405 possibly because the phylogenetic diversity score method used in our models may have missed  
406 important functional distinctions between closely related species (e.g. deciduous English oak and  
407 evergreen Holm oak). Life history strategy (e.g. pioneer vs late successional species) and shade  
408 tolerance have been used in other studies to gain insights into the influence of functional diversity  
409 (Niinemets & Valladares, 2006; Rüger et al., 2020; Williams et al., 2020), however a lack of available  
410 data for all the focal species considered in primary studies included in our meta-analysis prevented  
411 the inclusion of these metrics into meta-regression models.



412 In agreement with a previous meta-analysis by Richards et al. (2010), leaf nitrogen was significantly  
413 increased in diverse neighbourhoods that contained N-fixers. Conversely, phenolics were reduced in  
414 plants growing in neighbourhoods containing N-fixers, which could be interpreted as evidence of  
415 growth-defences trade-offs, although only partial support for interspecific growth-defence trade-offs  
416 has been found in studies included in this meta-analysis that also measured plant growth (Moreira et  
417 al., 2014; Rosado-Sánchez et al., 2018b; Walter et al., 2012).

#### 418 **Implications of leaf trait shifts in species mixtures**

419 Our study showed that the response of leaf traits to neighbourhood diversity is highly heterogeneous  
420 and may contribute to either increased or decreased leaf quality for herbivores, depending on the  
421 context. When paired with meta-analyses by Barbosa et al. (2009) and Jactel et al. (2021) that found  
422 that insect herbivory and abundance is on average lower in species mixtures than in monocultures,  
423 our findings indicate that leaf trait variation is not a dominant mechanism in mediating reductions in  
424 herbivory between diverse neighbourhoods.

425 However, despite finding overall negative effects of neighbourhood diversity effects on herbivory,  
426 both meta-analyses by Barbosa et al. (2009) and Jactel et al. (2021) demonstrated high degrees of  
427 heterogeneity and revealed numerous instances of increased herbivory and herbivore abundance in  
428 species mixtures. Our findings may offer novel insights here, as we revealed several circumstances  
429 where trait variation in diverse neighbourhoods could positively influence leaf quality for herbivores.  
430 For instance, increased SLA in mixtures with high species richness, or increased N and decreased  
431 phenolics in neighbourhoods containing N-fixers could increase the leaf quality of a focal plant and  
432 potentially offset the negative effects of reduced plant apparency and increased predation from  
433 natural enemies. The advantages of increased leaf quality could be particularly strong for generalist  
434 herbivores, which are often less sensitive to neighbourhood diversity effects due to a broader diet  
435 range, and may even benefit from a mixed diet (Jactel et al., 2021).

436 In addition to resistance to herbivory, leaf trait variation may also contribute to differences in plant  
437 fitness and productivity in different neighbourhood types (Davrinche & Haider, 2021; Proß et al., 2021;  
438 Zeugin et al., 2010). Plants in diverse neighbourhoods often exhibit increased productivity compared  
439 to those in monocultures (Feng et al., 2022; Tilman et al., 2001), which might in part be due to a shift  
440 towards more acquisitive leaf trait profiles that maximise photosynthesis and growth (e.g. high SLA  
441 and N, low LDMC, C and phenolic defences). We found only partial evidence of an acquisitive trait shift  
442 in diverse neighbourhoods, with SLA increasing with species richness and phenolics decreasing and N  
443 increasing in certain neighbourhood types (e.g. with N-fixers). Davrinche & Haider (2021) recently  
444 assessed the leaf trait responses of 16 tree species in a subtropical diversity experiment and found

445 that immediate conspecific neighbours shifted leaf traits into an acquisitive direction more strongly  
446 than neighbourhood diversity on a plot-level, which may partially explain why evidence for this  
447 phenomenon varied in this meta-analysis.

#### 448 **Future work**

449 This meta-analysis was limited to the examination of eight leaf traits as there was insufficient data  
450 available on other defensive and nutritional leaf traits such as alkaloids and sugar content (Table S1),  
451 as well as on other plant parts. Although seminal biodiversity studies were conducted in grasslands  
452 (Tilman et al., 2001), studies addressing effects of neighbourhood diversity on leaf traits of herbaceous  
453 plants are underrepresented in the literature, and several of the models in this analysis had to be  
454 restricted to data on trees. Finally, the genotypic diversity of a neighbourhood may have similar effects  
455 on plant traits to species diversity, but received insufficient attention in the literature to be considered  
456 in this study (but see Hoeber et al. 2017; Moreira et al. 2014; Weih et al. 2021).

457 We encourage future studies to explore the areas highlighted above, and to further investigate diverse  
458 neighbourhoods with characteristics that were under-represented in our meta-regression models,  
459 (mature trees, high species richness levels, high phylogenetic diversity).

460 More broadly, a deeper understanding of neighbourhood diversity effects on leaf traits could be  
461 gained if researchers were to account functional diversity within different species mixtures, such as  
462 differences in life-history strategies and shade tolerance, in addition to including measurements of  
463 abiotic factors known to effect leaf traits including light availability and soil moisture.

464

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## 700 **Supporting information**

701 Additional supporting information may be found in the online version of this article.

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## 704 **Data sources for the meta-analysis**

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